

Matías Reolid · Christian Gaillard · Federico Olóriz ·
Francisco J. Rodríguez-Tovar

Microbial encrustations from the Middle Oxfordian-earliest Kimmeridgian lithofacies in the Prebetic Zone (Betic Cordillera, southern Spain): characterization, distribution and controlling factors

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Abstract Two main types of microbial encrustation were identified in Middle Oxfordian to lowermost Kimmeridgian deposits in the Prebetic Zone (southern Spain), showing existing relationships between skeletal content, fabric and morphology of these organosedimentary structures. Laminated planar and concentric encrustations relate to peloidal fabrics (mainly constituted of microbes = microbial laminated fabrics s. str. and microbial oncoids s. str.), as well as to dense microbial fabrics periodically colonized by encrusting foraminifera (microbial laminated fabrics with nubeculariids and microbial oncoids with nubeculariids). Sedimentation rates, substrate stability and grain size, as well as illumination, influenced microbial growth pattern as major controlling factors in low-energy conditions, and forced palaeogeographic and stratigraphic patterns of distribution. Significant encrustation was identified in terrigenous-poor lithofacies from the middle (Transversarium-Bifurcatus zones) to the outer (Transversarium-Bimammatum zones) shelf in the Prebetic Zone. Rare-to-absent encrustation characterized terrigenous-rich deposits (Bimammatum and Planula zones) in the area.

Keywords Microbialite · Encrustation · Shelf environment · Upper Jurassic · Prebetic · Southern Spain

Introduction

The existence of carbonates related to microbial origin in Oxfordian sedimentary rocks in the Prebetic domain has previously been interpreted in relation to the presence of oncoids (García-Hernández et al. 1981; Olóriz et al. 2002a, 2002b) and buildups (Acosta et al. 1988; Acosta 1989, Martín-Algarra et al. 1990; Olóriz et al. 2003a, 2003b, 2003c). Initial studies of microbial carbonates or microbialites focused on stromatolites, and different terms were used by diverse authors for the microbiota involved: cyanophytes or cyanophycean algae (García-Hernández et al. 1981); cyanobacteria (Acosta et al. 1988); cyanophycean algae and bacteria (Acosta 1989). Recently, Oxfordian microbial carbonates in the External Prebetic have been analysed in relation to bioclast encrustation (Olóriz et al. 2003a; Reolid 2003) and the development of sponge bioherm-microbial lithoherm complexes (Olóriz et al. 2003b, 2003c; Reolid 2003). A detailed analysis of these microbial encrustations (characterization and interpretation) is of great interest in establishing the environmental framework existing during their development.

The purpose of this study is to characterize these microbialites by means of macroscopic and microscopic approaches, analysing their distribution in the depositional area (proximal to distal shelf environments) and interpreting the factors controlling their settlement, morphology and growth.

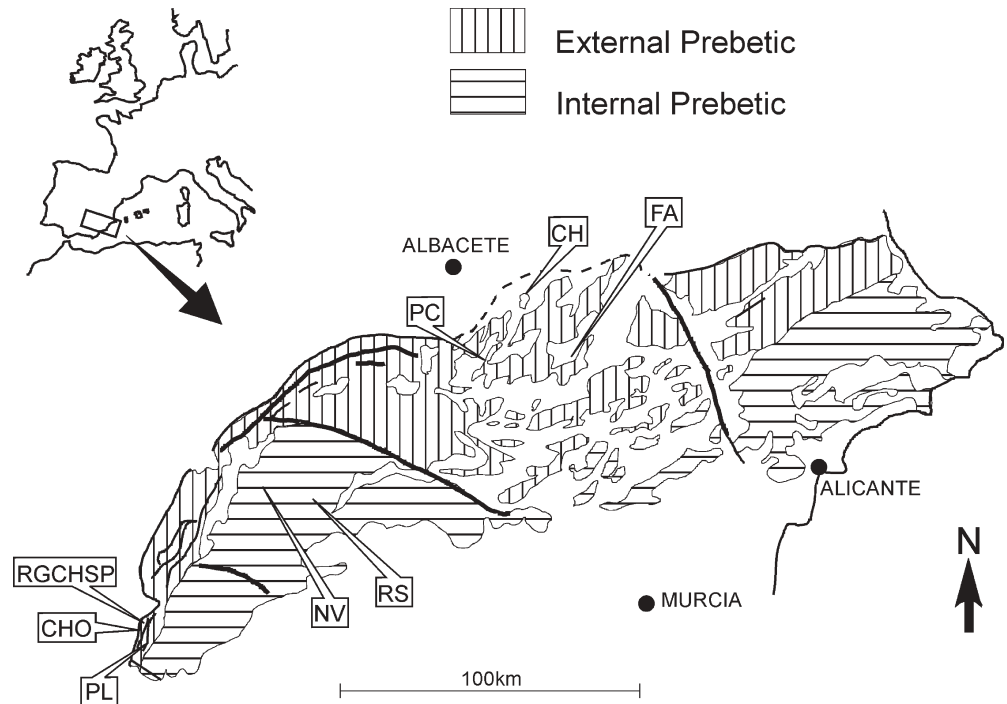
Geological context

The studied area is the outermost, northern sector of the Betic Cordillera, termed the Prebetic Zone (Fig. 1). Palaeogeographically, it constitutes part of the epicontinental carbonate and carbonate/siliciclastic marine shelf that developed at the SSE margin of Iberia during the Mesozoic. On the basis of stratigraphic and tectonic data, the Prebetic Zone is subdivided into the External and Internal Prebetic (Jerez-Mir 1973), which correspond to proximal

M. Reolid (✉) · F. Olóriz · F. J. Rodríguez-Tovar
Departamento de Estratigrafía y Paleontología,
Facultad de Ciencias,
Universidad de Granada, Campus Fuentenueva,
18071 Granada, Spain
e-mail: mreolid@ugr.es

C. Gaillard
UMR CNRS Paléoenvironnements et Paléobiosphère,
UFR des Sciences de la Terre,
Université Claude Bernard Lyon I, Géode,
2 rue Raphaël Dubois, 69622 Villeurbanne cedex, France

Fig. 1 Geological setting and location of sections: RGCHSP, Riogazas-Chorro; CHO, El Chorro; PL, Puerto Lorente; NV, Navalperal; RS, Río Segura; CH, Chinchilla; PC, Pozo Cañada; FA, Fuente Alamo



and distal parts of the neritic shelf, respectively. Prebetic outcropping areas may also refer to a central sector corresponding to Sierra de Cazorla and Sierra de Segura, and to an eastern sector east of these reliefs (Olóriz and Rodríguez-Tovar 1992). Eight sections were selected, six from the External Prebetic (Riogazas-Chorro, El Chorro and Puerto Lorente in the central sector, and Pozo Cañada, Chinchilla and Fuente Alamo in the eastern sector), and two from the Internal Prebetic (Río Segura and Navalperal; Fig. 1).

The succession studied corresponds to the Middle-Upper Oxfordian (Transversarium to Bimammatum zones), and locally ranges into the lowermost Kimmeridgian (Planula Zone; Fig. 2). These deposits fossilize a discontinuity surface (“complex unconformity” in Marques et al. 1991) situated at the top of oolitic limestones and dolostones belonging to the Lower-Middle Jurassic (García-Hernández et al. 1989). The upper boundary is biostratigraphically recognized either within the marl-limestone rhythmite lithofacies that includes the lowermost Kimmeridgian or in the omission surface (locally hardground) that precedes both the marl-limestone rhythmite lithofacies and the marl lithofacies. In the Prebetic Zone, the Middle Oxfordian-Lowermost Kimmeridgian varies in thickness between 0.5 and 23 m (Fig. 2). Seven lithofacies were differentiated into four lithofacies groups (Olóriz et al. 2003c; Reolid 2003): lumpy lithofacies group (lumpy limestone lithofacies, lumpy-oncolitic limestone lithofacies and condensed lumpy-oncolitic limestone lithofacies); spongiolithic lithofacies group (spongiolithic limestone lithofacies and spongiolithic marl-peloidal limestone lithofacies); marl-limestone rhythmite lithofacies group (marl-limestone rhythmite lithofacies); and marl lithofacies group (marl lithofacies). In the sector

studied, spongiolithic lithofacies and marl-limestone rhythmite lithofacies dominate in the proximal shelf registered (External Prebetic), while lumpy lithofacies are typical in more distal settings (Internal Prebetic). The marl lithofacies mainly occurs in the Planula Zone (lowermost Kimmeridgian) of the External Prebetic. Buildups containing microbialites have been recorded locally in both the marl-limestone rhythmite and the spongiolithic limestone lithofacies (Olóriz et al. 2002c, 2003b, 2003c; Reolid 2003), being more frequent in the former.

In most of these lithofacies, microbial encrustations have been documented, showing a clear differentiation in microbial activity concerning both stratigraphy (from Middle Oxfordian to lowermost Kimmeridgian) and paleogeography (proximal-to-distal gradient).

Microbialites

General considerations

The organic encrustations studied, mainly of microbial origin, are designated “microbialites” (Burne and Moore 1987). On the other hand, we use the term “microbial fabric”, which is equivalent to “cryptalgal fabric” as used by Monty (1976) and Flügel (1982).

The present study of microbial carbonates in the Prebetic Zone is carried out using macroscopic and microscopic approaches. Three types of microbial macrofabrics can be differentiated: stromatolites, thrombolites and leiolites, with leiolites and stromatolites being the most abundant (Olóriz et al. 2003c).

In accordance with the recent review of the subject by Riding (1999), we use the term “stromatolite” following

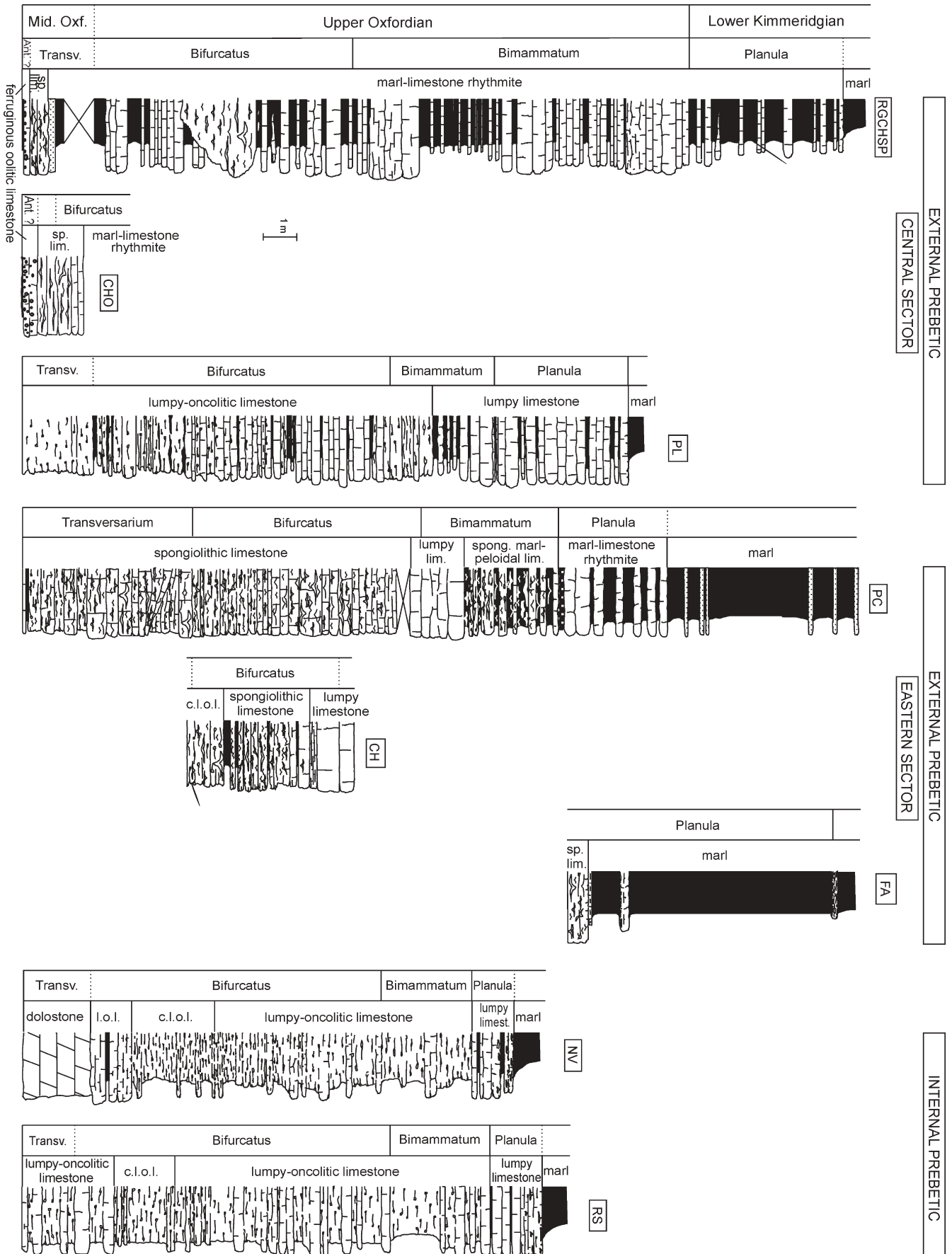


Fig. 2 Selected lithologic columns of different sectors studied showing ammonite bio-chronostratigraphy. Note: *col* for condensed lumpy-oncolitic limestone lithofacies, and *lol* for lumpy-oncolitic limestone lithofacies. See location of sections in Fig. 1

Table 1 Classification of Oxfordian-lowermost Kimmeridgian microbialites from the Prebetic Zone according to microscopic features

Morphology	Fabric		Most important organisms
Concentric (oncooids)	Laminated	Peloidal Micritic	Microbial s. str. (BMC) Nubeculariid (foraminifera)
Planar	Laminated	Peloidal Micritic Granular	Microbial s. str. (BMC) Nubeculariid
Columnar	Massive Laminated	Micritic Peloidal Micritic	Microbial (BMC) Microbial s. str. (BMC) Nubeculariid (foraminifera)

the original definition of Kalkowsky (1908). In the study area, stromatolites exhibit a macroscopic internal structure composed of thin laminae which have a more or less regular organization. The maximum thickness recorded is 75 mm, and a planar disposition is usually found. Finger-like columns develop, locally, from the initial planar mat.

The term “thrombolite” was proposed by Aitken (1967), but it is still controversial (Shapiro 2000). We consider thrombolites to be microbialites with an irregular internal structure and bushy morphology. Under the microscope, they have a clotted fabric, with millimetric to centimetric clots separated by patches of micrite, sand-size sediment or sparry cement (Kennard and James 1986). Patches of nonmicrobial micrite are lighter coloured than the clots and represent background sedimentation characterizing a buildup environment. Sparitic cement is related to geopetal structures.

Leiolites are microbial deposits with a structureless macrofabric (Braga et al. 1995; Riding 2000), although a laminated fabric has been identified under microscope.

Microbial encrustation has been registered on very diverse surfaces, and may be classified according to microscopic morphology, fabric and the most important associated encrusting microorganisms (Table 1). According to their morphology, three types of microbial encrustation can be differentiated: concentric, planar and columnar, the latter two being less abundant. Microfabric analysis allows us to distinguish laminated, nonlaminated and massive fabrics.

Main microbial structures

Concentric encrustations

These correspond to oncooids, which are the most common coated grains in the lithofacies studied. Other coated grains, both carbonate (ooids) and noncarbonate (ferruginous oolithes and pisolithes), only appear locally and are not considered here.

The term “onkoide” was initially proposed by Heim (1916). For Kimmeridgian examples from the Jura, Dahanayake (1977) defined “oncooid” as: “it is a simple body with a central nucleus and an envelope of concentric laminations which is sometimes called a cortex”. However, Flügel (1982) considered “oncooids” as “irregularly formed particles with nonconcentric, partially overlapping micritic laminae, derived from biogenic deposition

around a nucleus by algae, foraminifera, etc. mm- to cm-sized”. In these definitions, oncooid refers to a very general and imprecise concept, which favoured its use for grains with very different sizes, organizations and origins.

In the deposits from the Prebetic, oncooids are characterized by a nucleus and a mostly polyphasic coat (Fig. 3). Their usual oncooid morphology is spherical to ovoidal, but sometimes very irregular, depending on the grains forming the nucleus and on the type of envelope. The nucleus may be either a bioclast (e.g. crinoid ossicles, bivalves or ammonoid fragments, small ahermatypic corals) or nonskeletal grains (lumps, tuberooids, ooids). It is normally located in a central position, but sometimes occupies a marginal position due to more active encrustation extending in a preferential direction. According to the proportion of organisms forming the coating, two kinds of oncooids are differentiated: microbial oncooids s. str. and microbial oncooids with nubeculariids.

Microbial oncooids s. str.

These correspond to “micritic oncooids” or “algal oncooids” as described by Flügel (1982), and to the smooth oncooids (“oncoïdes lisses”) described by Gaillard (1983). They are mainly produced by microbes and their lamination is regular and well developed. These oncooids are constituted of episodic microbial growths, possibly due to cyanobacteria, with selective trapping of small micritic particles (Fig. 3a). The mean size of the oncooids is 2 mm, and they are no thicker than 3.5 mm. Their coating consists of alternating light and dark laminae. As shown by Massari (1981), the light laminae with a granular appearance are probably related to sediment-trapping mechanisms using a mesh of cyanobacterial filaments. Grains forming the light laminae are small peloids and micritic particles smaller than 30 µm (peloidal laminated fabric). The matrix between the grains is affected by epigenisation revealing fine microsparite. The dark laminae are thinner. The alternation of texturally different laminae may depend on the interaction between growths of benthic microbial communities (BMC) and periodic influxes of detrital particles (Monty 1976; Massari 1983).

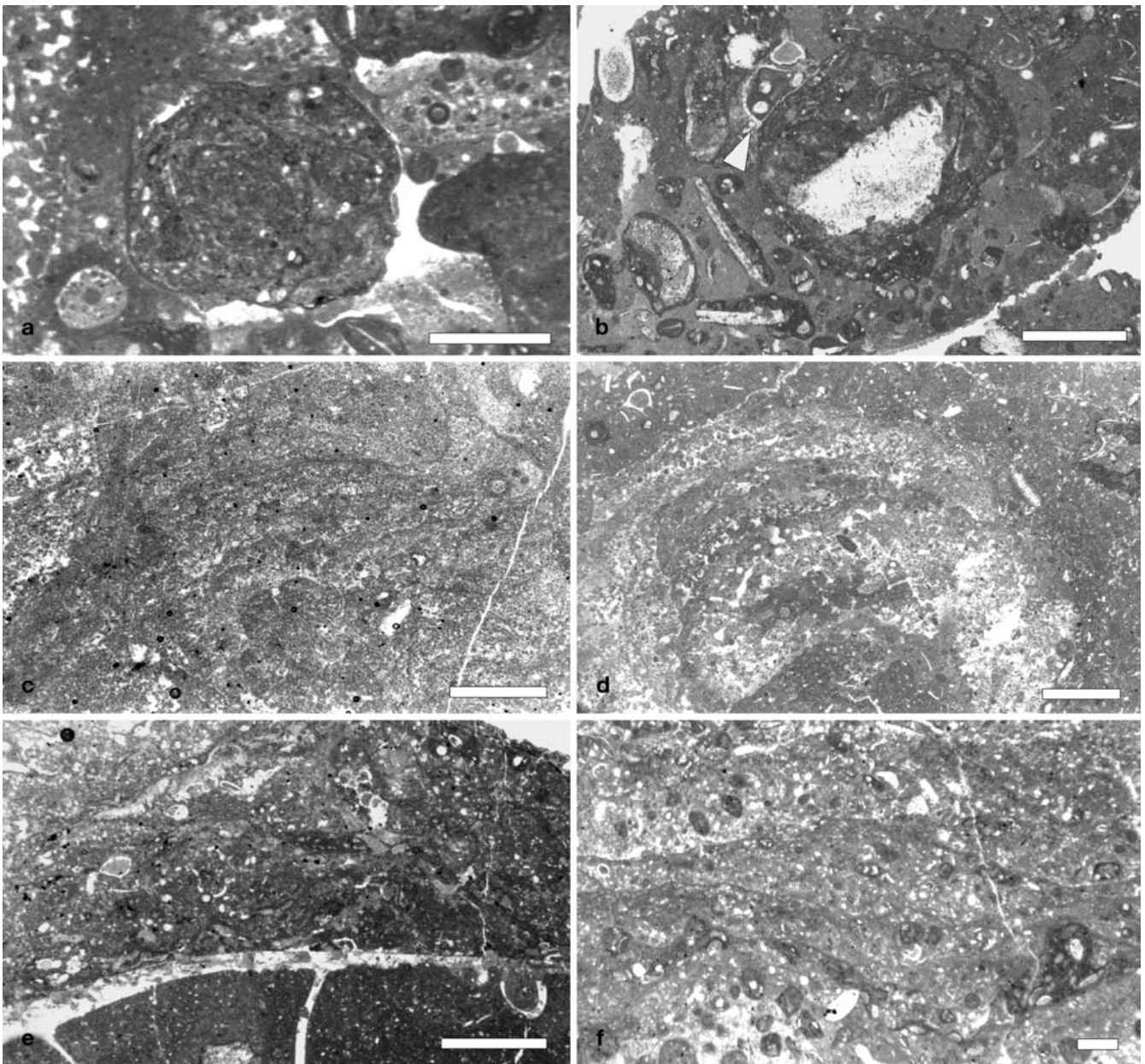


Fig. 3 Oncoids and microbial lamination (concentric and planar encrustation) in Oxfordian lithofacies from the Prebetic, southern Spain. **a** Microbial oncoids s. str. or smooth oncoids with local encrustation of nubeculariids. Lumpy-oncolitic limestone lithofacies, Internal Prebetic, Bifurcatus Zone (Upper Oxfordian). *Bar* 1 mm. **b** Microbial oncoid with nubeculariids or rough oncoid. The nucleus is a microbored fragment of echinoderm. *Arrow* *Bullopora tuberculata*. Other bioclasts show colonization by nubeculariids. Lumpy-oncolitic limestone lithofacies, Internal Prebetic, Bifurcatus Zone (Upper Oxfordian). *Bar* 1 mm. **c** Microbial laminated fabric s. str. with clotted peloidal microfabric. Lumpy-oncolitic limestone lithofacies, Internal Prebetic, Bimammatum Zone (Upper Oxfor-

dian). *Bar* 1 mm. **d** Microbial laminated fabric s. str. with clotted peloidal microfabric on dictyid sponge. Lumpy-oncolitic limestone lithofacies, Internal Prebetic, Planula Zone (lowermost Kimmeridgian). *Bar* 1 mm. **e** Microbial laminated fabric with nubeculariids on microperforated ammonite shell (*lower left*). Fabric subtype: micritic and clastic-skeletal poor fabric. Lumpy limestone lithofacies, Internal Prebetic, Bifurcatus Zone (Upper Oxfordian). *Bar* 1 mm. **f** Microbial laminated fabric with nubeculariids. Fabric subtype: clastic-skeletal granular fabric. Lumpy limestone lithofacies, Internal Prebetic, Planula Zone (lowermost Kimmeridgian). *Bar* 1 mm

Microbial oncoids with nubeculariids

Microbial oncoids with nubeculariids are larger, more complex and occur more frequently than microbial oncoids s. str. The former correspond to both the “zoogenic

oncoids” described by Flügel (1982) and the rough oncoids (“oncoïdes rugueux”) described by Gaillard (1983). They consist of grains with a biogenic coat that is mainly composed of nubeculariids associated with BMC. Their irregular aspect is due to the presence of dominant

nubeculariids and other sessile foraminifera (Fig. 3b). Microbial oncoids with nubeculariids present a mean size of 2.7 mm, reaching a maximum of 6.5 mm occasionally. The encrustations are darker than the encasing sediment. The coating of these grains features two zones, one very dark and irregular, corresponding to porcellaneous walls of nubeculariids, and another that is less dark and dense, assumed to be of microbial origin (micritic laminated fabric or “dense crust fabric” s. Leinfelder et al. 1993a). These oncoids relate to the colonization of grains by sessile foraminifera (mainly nubeculariids) associated with BMC (cyanobacteria?). The repetition of this process produced the different coatings and their laminated aspect, while smaller grains may be trapped between laminae forming the oncoid. Some microbial oncoids with nubeculariids include glaucony (s. Odin and Matter 1981) or iron oxides within the chambers of nubeculariids, usually located in a single lamina.

Planar encrustations

These are encrustations developed on more or less planar surfaces, which usually correspond to dish-shaped sponges, ammonoids or large intraclasts (Fig. 4). They are characterized by strong lateral and moderate vertical development. The encrustations are commonly less than 15 mm thick, but can reach 75 mm in sponge buildups (Olóriz et al. 2003c). Laminated and massive (= non-laminated) encrustation has been differentiated under microscope.

Laminated fabrics

Laminated fabrics result from grain size alternation visible in the encrustation (“laminated fabrics” s. Flügel 1982 described in the context of “cryptalgal fabrics”). Microbialites with laminated fabrics dominate on both the stromatolites and the leiolites located in buildups in the Prebetic Zone. As identified for concentric encrustations, the planar encrustation with laminated fabrics can be constituted of BMC or of consortia made up of BMC and sessile foraminifera (nubeculariids). Thus, differentiation of two laminated fabrics is possible according to the dominant organisms: microbial laminated fabric s. str. and microbial laminated fabric with nubeculariids (Fig. 5):

1. Microbial laminated fabrics s. str.: Microbial lamination consists of alternating light and dark laminae (Fig. 3c, d). The light laminae are composed of very small peloidal grains with pseudospherical microstructure (maximum size of 20–30 µm) and small micritic particles (“clotty structure” s. Monty 1967; “clotted, peloidal microfibrils” s. Gaillard 1983; Dromart et al. 1994; “minipeloidal fabric” s. Reitner and Schumann-Kindel 1997) surrounded by microsparitic matrix (“sparitic peloidal crust fabrics” s. Leinfelder et al. 1993a). As in the examples described by Massari

(1983), some light-coloured laminae show upwards decreasing size of peloidal microstructure and the opposite trend for particle density, which results in progressive darkening and termination with a thin, dark lamina. The lighter laminae are thicker (several millimetres) and laterally variable and they frequently pinch out. According to Riding (1991), the lighter, thicker laminae correspond to the trapping of small particles by the activity of benthic microbial mat communities. Riding (2002) proposes the term “agglutination” for “trapping” and “binding”. According to Reitner and Neuweiler (1995), a slightly allochthonous carbonate sedimentation rate helps in the building of mounds, which are stabilized by microbial mat trapping (“allomicrite”), while a very low level of background sedimentation produces encrustations where massive fabrics dominate (“automicrite” or “aphanitic automicrite” s. Reitner and Schumann-Kindel 1997). However, we cannot reject the possible formation of micropeloids, in the laminated fabric with peloidal microstructure, associated with organic matter degradation by build-up-reducing bacteria (Schumann-Kindel et al. 1997; Reitner and Schumann-Kindel 1997).

Within these laminated frameworks, circular or elliptical areas have been observed, which are envisaged as corresponding to boring activity (hollows cutting the lamination and filled with micritic sediment). Only locally, some laminae may be colonized by foraminifers and small annelid tubes.

2. Microbial laminated fabrics with nubeculariids. The microbial laminated fabrics with nubeculariids mainly consist of consortia of BMC and encrusting foraminifera (nubeculariids) (Fig. 3e, f). Two subtypes of microbial laminated fabrics with nubeculariids have been differentiated (Reolid 2003) including (1) micritic and clastic-skeletal poor fabric; and (2) clastic-skeletal granular fabric.

The most common microbial laminated fabric with nubeculariids is the micritic and clastic-skeletal poor fabric (Fig. 3e), which has thin laminae of dark-coloured micrite of microbial origin colonized by encrusting foraminifera, mainly nubeculariids. The organization of these laminae is similar to that shown by the microbial oncoids with nubeculariids. These laminae may show local colonization by annelids and bryozoa.

The clastic-skeletal granular fabric is less common (Fig. 3f). The laminae are very thick (normally exceeding 1 mm) and separated by thin laminae constituted of BMC and nubeculariids. The thick laminae are composed of a large quantity of heterometric grains (bioclasts, small lumps, ooids and peloids) with no particular spatial distribution. The clastic-skeletal granular fabrics are more irregular regarding the thickness and morphology of the granular laminae, as well as the size of the grains they trap.

Massive fabrics

The biogenic encrustations with nonlaminated or with massive fabrics (Flügel 1982) have been called “biogenic crust” (Flügel and Steiger 1981; Schorr and Koch 1985; Leinfelder et al. 1993a) and “cryptobacterial crust” (Riding 1991). The massive fabrics are composed of dense, homogeneous, cryptocrystalline micrite, which is identified by its dark colour, compared to the surrounding micrite. The massive fabrics of the Prebetic are similar to the “crusts” described by Matyszkiewicz (1989) in Upper Oxfordian cyanobacterial-sponge limestones from Poland.

Columnar encrustations

The microbial encrustations with columnar morphology occur locally (Fig. 5a). This morphology occurs in buildups (sponge bioherms-microbial lithoherms s. Olóriz et al. 2003c) found in the central sector of the External Prebetic. On the upper surface of the sponges, planar and locally club-shaped microbial over-growths, and locally finger-like columns, develop from an initial planar mat (Fig. 4a). The columnar structures are normally less than 11 mm wide and 33 mm high. Isolated columns occasionally occur on small substrates in the surroundings of buildups. The columnar encrustations always show laminated fabric, mainly microbial laminated fabric s. str. with laminae slightly convex upward.

Encrusting organisms

The most important organisms forming encrustations are microbes, probably cyanobacteria (citations below). These organisms constitute microbialites through the trapping and/or binding of fine detritic sediment or carbonate precipitation (e.g. Massari 1983; Burne and Moore 1987; Leinfelder et al. 1993a, 1994).

Encrusting porcellaneous foraminifera such as *Nubecularia* and *Nubeculinella* (Nubecularidae) are commonly associated with microbial activity. These encrust all types of surfaces in the lithofacies with a lower terrigenous content. Except for oncoids, nubeculariids are located on the upper side of the substrates, mainly associated with the most stable ones, such as sponges and ammonoids. This distribution agrees with those observed by Palmer and Fürsich (1974) and Leinfelder et al. (1993a).

Accompanying encrusting organisms are mainly sessile foraminifera, annelids and bryozoa. The foraminifera are (Fig. 6): *Bullopora* (Polymorphinidae), *Tolypammmina* (Ammodiscidae), *Thurammmina* (Saccamminidae), *Subdelloidina* (Lituolidae) and the two problematic micro-encrusters *Tubiphytes* and *Koskinobullina*. These foraminifera appear in lithofacies where the nubeculariids are more common, mainly encrusting siliceous sponges. *Tolypammmina*, *Thurammmina* and *Subdelloidina* are ag-

glutinated foraminifera with a wall constituted of small quartz grains. The genus *Bullopora* is mainly represented by *Bullopora tuberculata*. *Tubiphytes morronensis* is common in the lumpy lithofacies group from the Internal Prebetic and participates in the microbial oncoids with nubeculariids. *Tubiphytes* has been interpreted as nubeculariid foraminifera symbiotic with microbial coating (Flügel 1981; Leinfelder et al. 1993a; Dupraz and Strasser 1999). In addition, colonies of *Koskinobullina socialis* have been identified in the microbial laminated fabric with nubeculariids identified in the spongiolithic limestone lithofacies. The systematic position of *Koskinobullina socialis* is enigmatic, presenting similar characteristics to red algae (Cherchi and Schroeder 1979, 1985) and foraminifera (Werner 1986).

Serpulids are usually small and mainly correspond to *Cycloserpula*, *Dorsoserpula* and, locally, to *Tetraserpula* and *Pentaserpula*. *Terebella* is also present in some microbial laminated fabrics. Bryozoa are represented mainly by *Plagioecia* and *Ceriocava*. Annelids, bryozoans and other epibionts are more frequently found on the surfaces opposite those featuring microbial encrustations (lower flanks of ammonoids, and surfaces of downward-oriented sponges).

Distribution of encrustations

Oncoids (concentric encrustations)

Oncoid distribution in the Prebetic Zone is related to paleogeography, stratigraphy and lithofacies. Microbial oncoids s. str. and microbial oncoids with nubeculariids are more abundant in the Transversarium and Bifurcatus zones (Middle-Upper Oxfordian) of the Internal Prebetic. Microbial oncoids with nubeculariids dominate, except in the lower part of the Bifurcatus Zone where the microbial oncoids s. str. may locally be found more frequently. There is a general upwards decrease in abundance of oncoids, especially in the External Prebetic, where they disappear in the Planula Zone (lowermost Kimmeridgian).

In relation to lithofacies (Fig. 7), there is a higher frequency of oncoids in the lumpy-oncolitic limestone (24% of the grains) and in the condensed lumpy-oncolitic limestone (23% of the grains), both belonging to the lumpy lithofacies group (Reolid 2003). These lithofacies are very well represented in the Internal Prebetic, as well as in distal areas of the central sector in the External Prebetic (PL section). Oncoids in the External Prebetic are also related to the spongiolithic limestone lithofacies (10% of the grains) where microbial oncoids with nubeculariids dominate. Oncoids are absent from other lithofacies of the External Prebetic, which present a higher terrigenous content (marl-limestone rhythmite, spongiolithic marls and peloidal limestone, and marls).

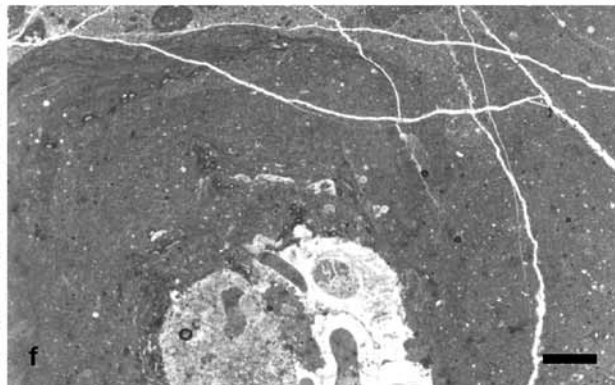
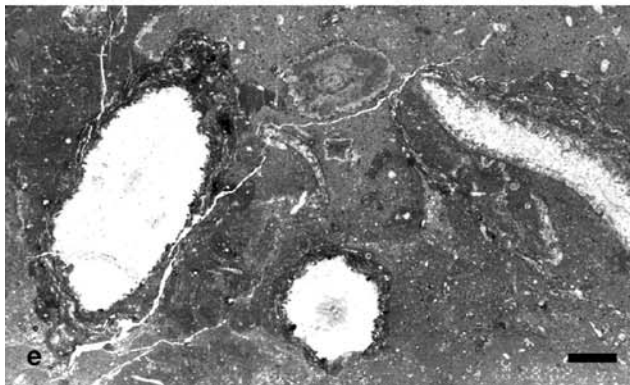
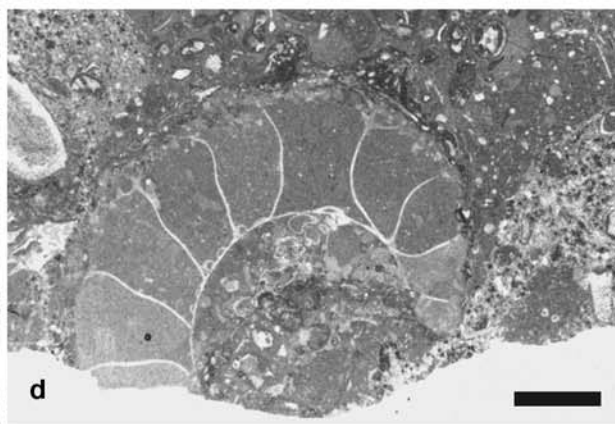
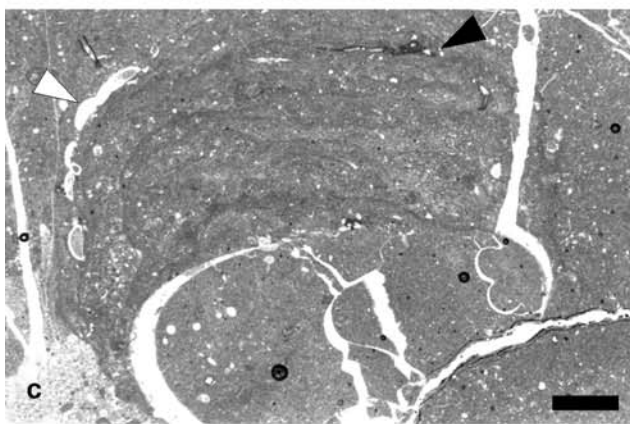
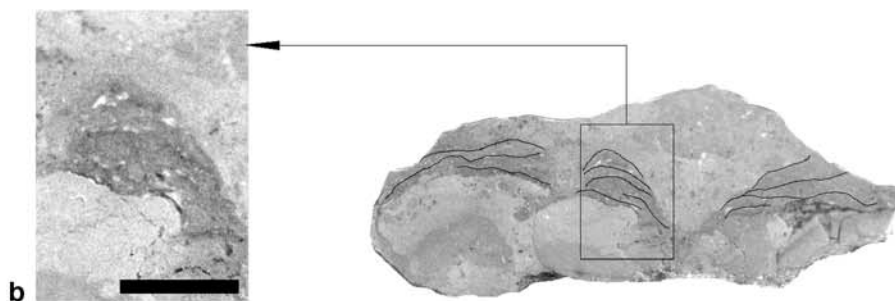
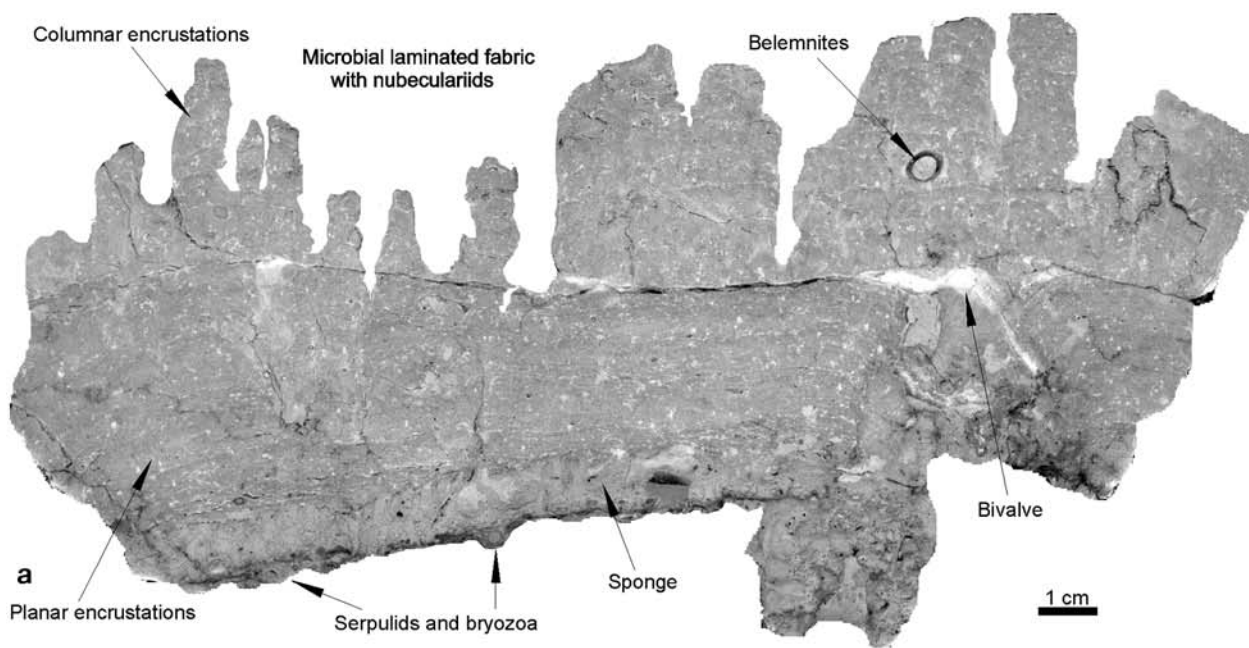


Fig. 5 Microbial encrustations on bioclastic substrates from spongiolithic limestone lithofacies. **a** Microbial laminated fabric s. str. with columnar morphology on small brachiopod shell. Benthic microbial communities (BMC). Spongiolithic limestone lithofacies, eastern sector of the External Prebetic, Bifurcatus Zone (Upper Oxfordian). Bar 1 mm. **b** Oblique section of coral in live position, fixed on serpulids (Se-1), and encrusted by serpulids (Se-2), bryozoa (Br) and benthic microbial communities (BMC). Spongiolithic limestone lithofacies, eastern sector of the External Prebetic, Bimammatum Zone (Upper Oxfordian). Bar 1 mm. **c** Conic sponge (dictyid) in a horizontal position (Sp). The lower side is encrusted by serpulids while the upper side develops microbial encrustation. Serpulids (Se) and *Terebella* (Tb) are located on protected surfaces. The upper side (downwards) shows benthic microbial communities (BMC). Spongiolithic limestone lithofacies, eastern sector of the External Prebetic, Bimammatum Zone (Upper Oxfordian). Bar 1 mm. **d** Typical distribution of encrusting organisms on *Terebella* remains (Tb). Serpulids (Se) on the lower side of *Terebella*, while benthic microbial communities (BMC) occupy the upper side. Spongiolithic limestone lithofacies, eastern sector of the External Prebetic, Bifurcatus Zone (Upper Oxfordian). Bar 1 mm

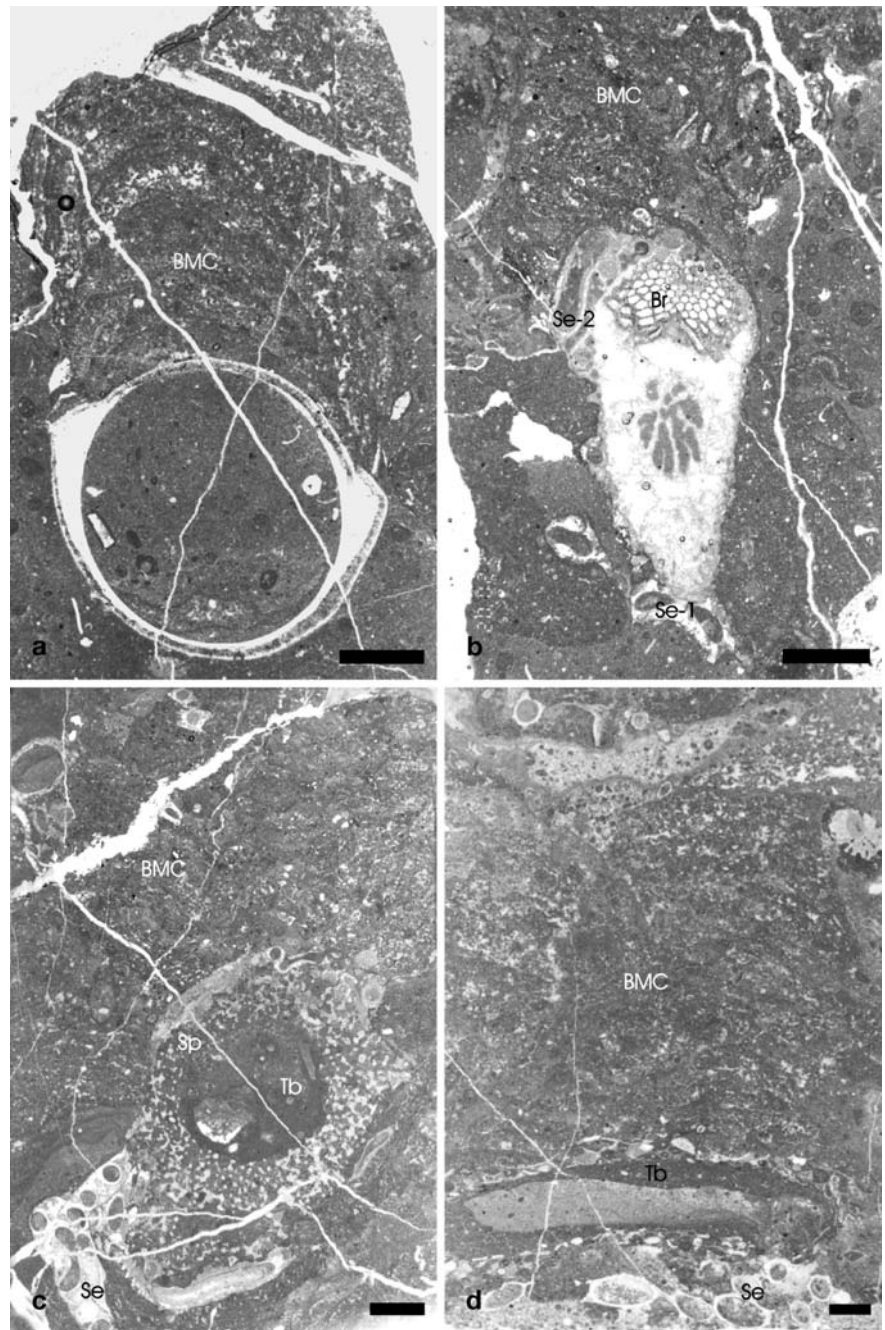


Fig. 4 Encrustations on different types of substrates. **a** Polish-transverse section of encrusted sponge showing microbial laminated fabrics with nubeculariids. Note *i* planar microbialite over sponge remains, *ii* variable upward development of club-shaped microbialites, *iii* serpulids and bryozoa on the lower surface of the sponge, and *iv* bivalves and belemnites included in microbialite framework. Buildup from marl-limestone rhythmite lithofacies, central sector of the External Prebetic, Bifurcatus Zone (Upper Oxfordian). **b** Polish axial section of *Dichotomoceras* showing microbial encrustation on its upper flank. Microbial growth is located on higher parts of the exposed surface of the mould (*external whorl*), while the umbilicus is plugged by micritic sediment. Condensed lumpy-oncolitic limestone lithofacies, Internal Prebetic, Bifurcatus Zone (Upper Oxfordian). Bar 1 cm. **c** Encrusted ammonite showing microbial laminated fabric s. str. and local colo-

nization by *Bullopore* (white arrow) and nubeculariids (*black arrow*). Spongiolithic limestone lithofacies, eastern sector of the External Prebetic, Bifurcatus Zone (Upper Oxfordian). Bar 1 mm. **d** Nubeculariid encrusting the upper surface of internal mould of ammonites. Lumpy-oncolitic limestone lithofacies, Internal Prebetic, Bifurcatus Zone (Upper Oxfordian). Bar 1 mm. **e** Corroded belemnites (Be) mainly encrusted by nubeculariids, and fragments of bivalves and echinoderms showing microboring. Spongiolithic limestone lithofacies, External Prebetic, Planula Zone (lowermost Kimmeridgian). Bar 1 mm. **f** Detail of microbial laminated fabric. Note colonies of nubeculariids encrusting the echinoid plate and serpulid colony. Spongiolithic limestone lithofacies, eastern sector External Prebetic, Planula Zone (lowermost Kimmeridgian). Bar 1 mm

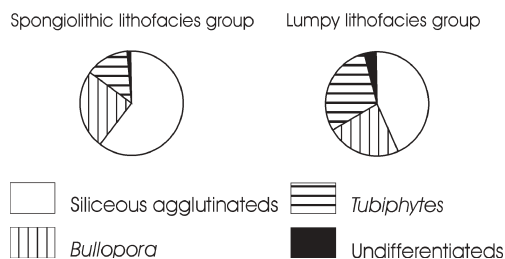


Fig. 6 Relative abundance of sessile, noncolonial foraminifera registered in major lithofacies groups showing encrustations (spongiolithic lithofacies group and lumpy lithofacies group)

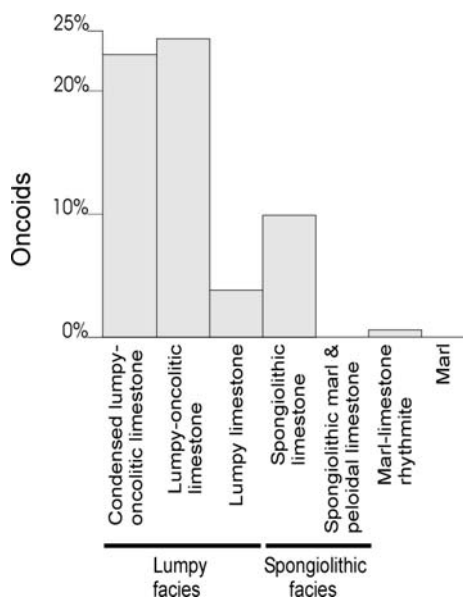


Fig. 7 Oncooid relative abundance (% in microfacies) in Oxfordian lithofacies from the Prebetic

Planar encrustations

Planar encrustations are scarcer than concentric ones, and mainly correspond to microbial laminated fabrics s. str. Concerning the microbial laminated fabrics with nubeculariids, the clastic-skeletal granular fabrics are the rarest. Evolution from microbial laminated fabric s. str. to microbial laminated fabric with nubeculariids is documented in some microbialites.

Planar encrustations appear in lithofacies with a lower terrigenous content, i.e. spongiolithic limestone in the more proximal sectors (External Prebetic) and lumpy-oncolitic limestone and condensed lumpy-oncolitic limestone in the more distal ones (Internal Prebetic). These encrustations present the best development in sponge bioherm-microbial lithoherm complexes located in the central sector of the External Prebetic (Sierra de Cazorla, province of Jaén), in the spongiolithic limestone and particularly in the marl-limestone rhythmite lithofacies (Olóriz et al. 2002c, 2003b, 2003c).

From a stratigraphic point of view, planar encrustations typically occur in the Transversarium and Bifurcatus zones of the External Prebetic, and locally within the Bimammatum Zone related to the distribution of spongiolithic limestone lithofacies and buildups. In the Internal Prebetic, planar encrustations appear throughout the studied stratigraphic range (Transversarium to Planula Zones), being more abundant in the lower part of the Bifurcatus Zone and in the Bimammatum Zone.

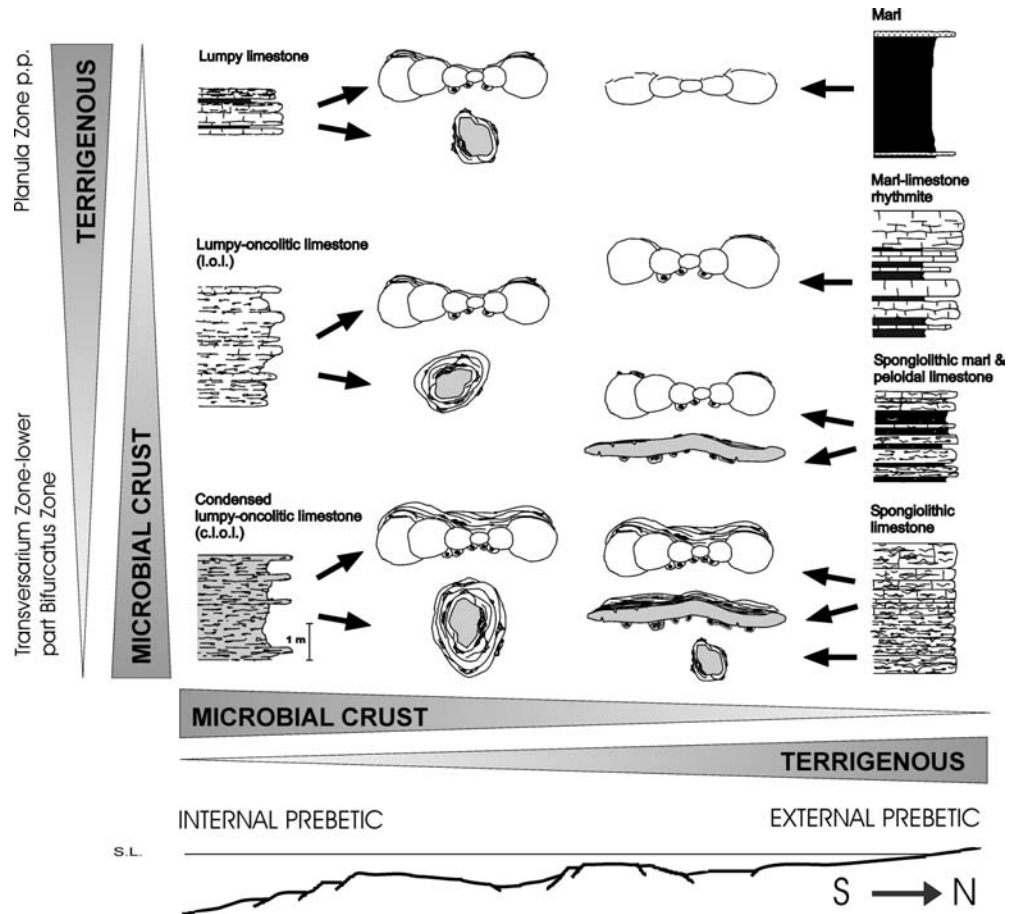
Encrusting organisms

The quantitative analysis of sessile benthic foraminiferal assemblages (excluding nubeculariids) reveals important differences according to the lithofacies groups (Table 2). In general, the highest values of sessile foraminifera correspond to the spongiolithic lithofacies group and to the lumpy lithofacies group, while the lowest values are found in lithofacies with a higher terrigenous content. Four groups can be differentiated: siliceous agglutinated forms (*Tolypammina*, *Thurammina* and *Subdelloidina*), *Bullopora*, *Tubiphytes* and undifferentiated sessile foraminifera. In the clastic-poor lithofacies, siliceous agglutinated foraminifera dominate (Table 2, Fig. 6); these are more abundant in the spongiolithic lithofacies group (60%) than in the lumpy lithofacies group (34%), while *Bullopora* presents similar proportions (24% and 23% respectively) in these lithofacies groups. *Tubiphytes* is predominant in the marl-limestone lithofacies group (71%) and in buildups (58%) (Table 2). Nevertheless, Reolid (2003) indicates that the high frequency of *Tubiphytes* found in the marl-limestone lithofacies group reveals fragmentation. Excluding the marl-limestone lithofacies, where sessile benthic foraminifera are scarce and a high degree of fragmentation exists, it is possible to study

Table 2 Composition of benthic foraminiferal assemblages in relation to the lithofacies studied, including buildups

	Marl-limestone rhythmite lithofacies group	Buildups	Spongiolithic lithofacies group	Lumpy lithofacies group
Vagile benthic foraminifera	93%	82%	85%	85%
Sessile benthic foraminifera	7	18	15	15
<i>Tolypammina</i>	8.8%	10.8%	30.2%	14.2%
<i>Thurammina</i>	0	10.8	10.4	8.2
<i>Subdelloidina</i>	0	3.1	19.4	11.4
<i>Bullopora</i>	20.3	16.9	23.9	22.9
<i>Tubiphytes</i>	70.9	58.5	12.4	39.5
Undifferentiated	0	0	3.7	3.8

Fig. 8 Relative abundance of terrigenous and encrustation along the Prebetic shelf. Note clear differentiation in microbial activity (crusts), expressed both stratigraphically (from Middle Oxfordian to lowermost Kimmeridgian) and paleogeographically (proximal-distal gradient)



the distribution in a proximal-distal transect in the shelf. Thus, a reduction in siliceous agglutinant forms and an increase in *Tubiphytes* have been observed seawards.

Controlling factors

The settlement, morphology and growth of microbial encrustations seem to be related to three main factors: sedimentation rate/terrigenous content, substrate features and light availability.

Sedimentation rate/terrigenous content

The development of microbialites needs a low rate of sedimentation because their growth is very slow (e.g. Leinfelder et al. 1993a, 1993b, 1994; Brunton and Dixon 1994; Olivier et al. 2003). They are also very sensitive to any unfavourable influx of fine, clay-rich sediment. Thus, microbialites are good indicators of the rate of siliclastic influx. The columnar morphologies in the microbial encrustations reflect slight increases in the sedimentation rate (cf. Gaillard 1983; Dromart et al. 1994). Most encrustations are laminated, showing rhythmic growth of BMC, growth breaks being attested by colonization by nubeculariids and other epibionts. The low sedimentation

rate and the episodic growth are confirmed by the presence of laminae containing glaucony and iron oxide impregnations within microbial oncoids with nubeculariids as documented in the Planula Zone of the Internal Prebetic (Reolid 2003). Biogenic encrustation of microbial origin was lithified early, as revealed by the presence of encrusting foraminifera, serpulids and bryozoans in numerous concentric, planar and columnar structures. According to Leinfelder et al. (1993a), the frequency of sparitic peloidal crust fabrics, even within a general micritic setting, indicates early hardening of encrusting structures resulting from encrustation episodes. The occurrence of borings in some microbialites with microbial laminated fabric confirms quick lithification.

In the examples studied, the higher the frequency of oncoids, the lower the content of quartz and muscovite is developed, a relationship which, in general, applies to the content of fine, clay-rich sediments. This indicates that terrigenous influx was unfavourable for microbial growth (Fig. 8). The presence of nubeculariids is also indicative of a low sedimentation rate. This is confirmed by the upward (and landward) decreasing proportion of microbial oncoids with nubeculariids, in parallel with the increase in the rate of terrigenous influx. This relation has also been observed for the colonization of grains by sessile foraminifers, annelids and bryozoans, which are absent from marl and marl-limestone rhythmite lithofacies.

Therefore, the higher abundance of microbialites toward more distal sectors (Internal Prebetic) is consistent with the presence of low-energy, deeper environments in outer-shelf areas that developed in the South Iberian paleomargin during the Late Jurassic (Olóriz et al. 2002b). A similar trend has also been documented in other Late Jurassic shelf areas of western Tethys (Dromart and Elmi 1986; Dromart 1989, 1992; Gygi 1992). However, Dromart and Elmi (1986) established that these types of encrustations are not necessarily related to shallow water environments.

In the central sector of the External Prebetic, the occurrence of marl-limestone rhythmite lithofacies that contain buildups showing a huge development of encrustation with laminated fabrics is in apparent contradiction with the previous interpretations. As explained below, these buildups can be interpreted according to the model proposed by Gaillard (1983) for the “biohermes à spongiaires” found in southern Jura. The episodic colonization of the seabed by pioneer sponges provided the only favourable substrates for the growth of BMC. Thus, a preferential, local growth of microbial mats occurred in unfavourable muddy bottoms which resulted in local sponge bioherm-microbial lithoherm complexes.

Substrate features

The influence of the substrate on microbial encrustation cannot be considered in a single way, but rather as resulting from the interaction of multiple factors affecting colonization. Thus, substrate composition, particle size, shape and/or stability are some of the features determining the relevance of substrate as a limiting factor.

Substrate stability clearly controls the morphology of encrustation, and depends on two factors: environmental energy and substrate type (including morphology).

As a rule, the encrustations were formed in low-energy environments. However, the homogeneous development of encrustations around the nucleus in oncoids indicates the free movement of grains on the seafloor during colonization by encrusting organisms. The small size of oncoids indicates a moderate energy level. However, the presence of oncoids is not always indicative of water turbulence forcing occasional overturning. In fact, autochthonous growth in modern oncoids has been occasionally reported from lakes and lake margins (Jones and Wilkinson 1978; Dahanayake et al. 1985; Leinfelder and Hartkopf-Fröder 1990), but environmental conditions interpreted for the Prebetic shelf clearly differ from those described for the modern oncoids mentioned.

Substrate size is also a major factor affecting colonization by encrusting organisms. Small grains such as lumps, peloids, filaments and small foraminifera comprise an unfavourable support for colonization. They provide a limited surface available for encrustation, and are easily reworked and buried. In contrast, sponges and ammonites provide large, hard, favourable substrates and thus encrustation with planar morphology on the upward surface

is commonly found (Olóriz et al. 2002b, 2003c). Siliceous sponges are the largest biotic remains (mean size up to 20 cm) and provide large, favourable basements that are clearly visible in beds of spongiolithic limestone lithofacies. These, in turn, are characterized by large mean sizes of fossil macroinvertebrates and high encrustation proportions (Olóriz et al. 2002b, 2002c). In an intermediate situation, some large lumps, tuberoids and bioclasts formed oncoids, most probably due to the relation between bioclast size and environmental energy, permitting both episodic reworking and biotic encrustation.

The substrate morphology also determines its stability, potential colonization, and, finally, the resulting encrustation morphology, dish-shaped siliceous sponges being the most common, stable substrate.

According to the model proposed by Dromart et al. (1994) for Oxfordian sediments in the western margin of the French Subalpine basin and the Nova Scotia shelf (Canada), the ideal sequence reflecting a progressive stabilization of lumpy sediments includes four stages: isolated lumps, oncoidites, columnar stromatolites and planar stromatolites. Thus, lithofacies with a high abundance of lumps and oncoids, as registered in the Internal Prebetic, would indicate an intermediate situation, between the first two stages of substrate stabilization that reflect an environmental energy that is sufficient to form oncoids, but not enough to move larger-size substrates (sponges and ammonoids) in which encrustation with planar and columnar morphologies developed.

Light availability

Light is a fundamental factor favouring microbial encrustation, providing a major source of energy (but see modern examples from the Great Barrier Reef studied by Reitner, 1993). In the case study, encrustations with planar, slightly convex, columnar morphologies are found only on the exposed surfaces of sponges and ammonoids. This indicates both the upward growth and possible photophilic character of the BMC (Gaillard 1983, 1984). This specific location of encrustations on well-exposed surfaces can also be related to low-to-absent sedimentation (Keupp et al. 1993), which, therefore, can be termed an additional or complementary factor of light availability. The similar appearance of oncoids and planar and columnar encrustations allows us to envisage the role of positive phototropism in the development of concentric encrustations. Grains showing nuclei in a lateral position can be interpreted as resulting from differential exposure times, these being longer where encrustation is thicker.

On the contrary, the protected, less illuminated downward surfaces of sponges and ammonoids were mainly colonized by serpulids and *Terebella* (Olóriz et al. 2002a, 2002b, 2003c). This preferential colonization by serpulids can be interpreted as due to: (1) possible photophobic behaviour (Gaillard 1983; Fernández-López 1987); (2) the possibility of avoiding space competition with BMC activity (Palmer and Fürsich 1974; Gaillard

1983); and/or (3) avoiding predation. All of this agrees with Kobluk (1988), who interpreted these epibionts as a “cryptobiontic organism” living in habitats protected from direct exposure to light. In the case study, whatever the dominant forcing factor (or combination of factors), the growth of BMC was comparatively aggressive for other epibionts, which are either absent or thickly covered. Where thickly covered, the epibionts cannot be still alive and microbes withstand.

The analysis of sponges and other macroinvertebrate assemblages allows us to interpret photic conditions for the depositional setting, and assigns a depth of around 60 m for the External Prebetic and 80 m for the Internal Prebetic (Olóriz et al. 2002b, 2003c; Reolid 2003). A light intensity of 1–10% of surface light intensity can be assigned, according to Vogel et al. (1999).

Conclusions

The study of microbial encrustations in Middle Oxfordian to lowermost Kimmeridgian deposits in the Prebetic Zone (southern Spain) enabled us to differentiate two main types of biotic encrustation according to their morphology: concentric and planar, and secondarily columnar. Both laminated planar and concentric encrustations present two types of fabric: (1) peloidal fabric mainly constituted of microbes (microbial laminated fabrics s. str. and microbial oncoids s. str.); and (2) a dense microbial fabric periodically colonized by encrusting foraminifera (microbial laminated fabrics with nubeculariids and microbial oncoids with nubeculariids).

In the context of a low-energy environment, microbial encrustation features were mainly controlled by factors such as: (1) sedimentation rate, including the terrigenous content; (2) substrate features; (3) light availability. Variations in major limiting factors determined trends registered in the microbial features, both stratigraphically and paleogeographically. Thus:

- a. Terrigenous-poor lithofacies (lumpy-oncolitic limestone lithofacies and condensed lumpy-oncolitic limestone lithofacies) show significant encrustation, mainly materialized as oncoids and planar encrustations on more stable substrates (dish-shaped sponges and ammonoids). These lithofacies are documented in the Transversarium to Bimammatum zones in the Internal Prebetic, which represents outer shelf areas in south-to-south-eastern Iberia. In contrast, in the spongiolithic limestone lithofacies, planar encrustations predominate due to the high frequency of sponge remains. This lithofacies is dominant in the Transversarium and Bifurcatus zones of the External Prebetic, which represents a relatively proximal sector (mid-outer shelf) in the region.
- b. Lithofacies with a higher proportion of terrigenous (spongiolithic marl and peloidal limestone lithofacies, marl-limestone rhythmite lithofacies and marl lithofacies) are characterized by the absence of encrustations.

These lithofacies are developed in the comparatively most proximal sector that is preserved (mid shelf), and are better developed in the Bimammatum and Planula zones.

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